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Benthos of Adjacent Mangrove, Seagrass and Non-vegetated Habitats in Rookery Bay, Florida, U.S.A.

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Benthic faunal abundances and biomasses in adjacent mangrove, seagrass and non-vegetated mud habitats were compared in Rookery Bay, Florida, U.S.A. Although all habitats were intertidal, mangroves received the shortest duration of flooding, and non-vegetated mud received the longest. Replicate cores were taken at high tide in each habitat in July, September and December 1988, and in April 1989. Seagrass substrates were low organic content sands, whereas mangrove and non-vegetated substrates were high organic content sandy clays. Over 300 taxa were recorded, most of them relatively rare, and only 32 taxa were considered dominant (averaging $\geq$636 individuals m^{-2} or five core^{-1} in any habitat at a given time). Seagrass and non-vegetated mud faunas were more diverse than those of mangrove substrates. Total densities were always higher in red mangrove (*Rhizophora mangle*) peat than elsewhere, averaging 22 591 to 52 914 individuals m^{-2}. Densities in mixed seagrasses ranged between 6347 and 23 545 individuals m^{-2}, while those in non-vegetated mud ranged between 3611 and 22 465 individuals m^{-2}. Biomasses, however, were always higher in either seagrasses (15·7–87·4 g wet weight m^{-2}) or non-vegetated mud (11·9–26·2 g m^{-2}) than in mangroves (3·6–8·2 g m^{-2}). Tanaids and annelids were the numerical dominants, reaching maximum densities of 35 127 and 31 388 m^{-2}, respectively, in mangroves. Annelids were also the dominant biomass in most habitats each month. Variation in densities of most of the 32 dominant taxa were related to habitat not time. Each habitat harboured four to eight taxa that were significantly more abundant there than in alternate habitats. Feeding guild analysis indicated few differences among habitats, as surface deposit feeders and carnivores were predominant. Red mangrove appear capable of functioning in a manner similar to intertidal marsh habitats by providing high densities of small prey items for mobile consumers able to exploit the intertidal zone during high tide. Experimental verification of this function remains necessary.

Keywords: benthos; mangroves; seagrass; mud; habitats; estuaries; Florida

Introduction

Mangroves are the dominant intertidal vegetation of low energy shorelines in the tropics and subtropics (Chapman, 1977). In the continental United States, permanent mangrove habitat is found only in Florida (Sherrod & McMillan, 1985), where it is almost twice as extensive as emergent tidal marsh vegetation (Lewis *et al.*, 1985). The mangrove ecosystem of southern Florida, encompassing adjacent mangroves, seagrasses and non-vegetated mud, supports a variety of forage and commercially and recreationally important fishes and invertebrates (Odum *et al.*, 1982; Zieman, 1982; Tilmant, 1989). Fish and decapod densities among mangrove prop roots during some seasons are comparable to densities in alternative, nearby habitats (Thayer *et al.*, 1987; Sheridan, 1992; Ley, 1992; Thayer & Sheridan, 1997). However, benthic faunal communities inhabiting Florida's intertidal mangrove substrates, and their abundances relative to those in adjacent habitats, are poorly known (Odum *et al.*, 1982; Continental Shelf Associates, Inc., 1990). This situation is common worldwide (Alongi, 1989). Like seagrasses and emergent marshes, mangrove substrates may support higher densities of benthic prey for mobile predators than do adjacent non-vegetated substrates (Virnstein *et al.*, 1983; Lewis, 1984; Orth *et al.*, 1984; Edgar, 1990), resulting from higher predation pressure over non-vegetated substrates (Robertson, 1984; Summerson & Peterson, 1984) or lower predation pressure due to tide-limited access (Kneib, 1984) or both. The objective of this study was to quantify and compare densities of benthic infauna and epifauna among adjacent intertidal red mangrove (*Rhizophora mangle*), mixed seagrass and non-vegetated mud habitats in southern Florida.

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Methods

The Rookery Bay National Estuarine Research Reserve is located on the south-west coast of Florida near Naples. An estimated 47% of the 3400 hectare reserve is dominated by several species of mangroves, and 20% of the bay floor supports seagrasses (Yokel, 1975; Rookery Bay National Estuarine Research Reserve, 1986). Sampling sites were located in a 300 m diameter, semi-circular embayment in northern Johnson Bay (26°01'N, 81°44'W), along the southern edge of the reserve. Non-vegetated mud was found between seagrasses, located in the centre of the embayment, and red mangrove fringing the shoreline. Samples were collected from red mangrove, mixed seagrass and non-vegetated mud substrates during high tides. Seagrass and non-vegetated mud sites were chosen haphazardly, while red mangrove sites were fixed and were positioned 2–3 m into the prop root zone (in conjunction with macrofaunal sampling; Sheridan, 1992). All samples from a given habitat were taken at least 10 m apart but within 150 m of the centre of the embayment. All habitats were intertidal to some degree, with mangroves receiving the shortest duration of flooding and non-vegetated mud receiving the longest. Seagrasses were primarily shoal grass (*Halodule wrightii*), but included manatee grass (*Syringodium filiforme*), clover grass (*Halophila englemanni*) and turtle grass (*Thalassia testudinum*). Samples were collected in July, September and December 1988 and in April 1989, within a 3-day period each month. Measurements of salinity (by temperature-compensated refractometer and the Practical Salinity Scale), temperature (by stick thermometer) and water depth were made with each sample, with the exception of December when the refractometer failed after one measurement in each habitat.

Since there were no *a priori* data with which to determine local sampling effort, sample size was derived from a power analysis (Sokal & Rohlf, 1981) of 25 cores collected from a *H. wrightii* bed near Galveston, Texas (Sheridan, unpubl. data). With 8–10 samples per habitat, a 100% difference in means could be detected between two habitats with $\alpha=0{\cdot}10$ and $1-\beta=\text{power}=0{\cdot}75$ for total fauna and the expected dominant phyletic groups (Amphipoda and Annelida; Devlin *et al.*, 1987). Eight cores were collected per habitat each month, except in September when 10 cores were taken. Benthic infauna and epifauna were collected with a 10 cm diameter (78·5 cm^2 surface area) plastic corer to a depth of 10 cm, rinsed through a 0·5 mm mesh sieve, and preserved first in buffered 10% formalin-seawater containing rose bengal and later in 70% ethanol. Laboratory processing included identification to the lowest possible taxon and counting of individuals. Assignment of a letter code to certain species of annelids (e.g. *Ancystrosyllis* sp. C) follows Uebelacker and Johnson (1984). After identification, organisms were grouped by abundant phyla (Annelida, Mollusca), orders (Amphipoda, Isopoda, Tanaidacea) or as a group of less abundant phyla, classes and orders (Miscellaneous, including Turbellaria, Nemertinea, Mysidacea, Cumacea, Insecta, Sipunculida, Phoronida and Ophiuroidea), blotted and weighed to the nearest 0·1 mg to estimate biomass. Molluscs were removed from their shells prior to blotting. Hereafter, these groups are referred to as major phyletic groups.

An additional core was collected at each site for sediment analyses, except in December. Organic content was measured by loss on ignition (Dean, 1974), wherein a subsample was dried at 100 °C to a constant weight, then burned in a muffle furnace at 500 °C for 4 h and reweighed. Sand–silt–clay ratios were determined by shaking a subsample overnight in fine-sediment dispersant (2·55 g l^{-1} sodium hexametaphosphate), washing through a 0·063 mm mesh sieve to capture gravel- and sand-sized particles (combined as sand), and pipetting the washings for silt- and clay-size particles (Folk, 1980). Fraction weights were determined by drying at 100 °C to a constant weight.

Two-way ANOVA was used to assess effects of habitat and time on faunal density, species richness (defined as S-1/log n, where S=number of species or lowest identified taxon, and n=number of individuals), biomass and sediment characteristics. Abundant species or taxa (defined as those with counts averaging ≥ 636 individuals m^{-2} or five individuals $core^{-1}$ in any habitat in any given sampling period), major phyletic groups and total benthos were tested. One-way ANOVA was used to assess habitat effects on water column characteristics. Distribution of error terms for each abundant taxon and major phyletic group violated assumptions of normality, as indicated by the Shapiro–Wilk test statistic (Shapiro & Wilk, 1965). Positive relationships between means and variances were detected, and log $(x+1)$ transformation was used successfully to achieve homogeneity of variances. Distributions of error terms for water and sediment properties (after arc-sine transformation of organic, sand, silt and clay proportions) exhibited normality. When two-way ANOVA indicated only habitat or time effects and no interaction effect, data were pooled and re-evaluated by one-way ANOVA. Multiple comparison of treatment means employed Ryan's Q-test with $\alpha=0{\cdot}05$ (Day & Quinn, 1989). All analyses were conducted using SAS software programs (SAS Institute Inc., 1985). Tabular data are untransformed means, and faunal data are converted to a per square metre basis for comparative purposes.

Functional implications of patterns in faunal abundance were examined by an analysis of feeding guilds, in which food preference, motility pattern and feeding structure morphology are considered, as developed for polychaete families by Fauchald and Jumars (1979). Information for other taxa was derived from Barnes (1968), Schultz (1969), Odum and Heald (1972), Bousfield (1973) and Heard (1982).

Results

Water and sediment properties

Water temperatures ranged between 19 °C in December and 32 °C in July, while mean salinities were 31 to 37 (Figure 1). Although significant differences in mean temperatures among habitats were always detected (seagrasses usually had the lowest temperatures), the range in means was less than 2 °C in a given month. Significant differences in salinity were only detected in September. Mean water depths (Figure 1) ranged between 15 and 71 cm, were consistently greatest in non-vegetated mud, and were usually significantly shallower in red mangroves than elsewhere.

Sediment properties were significantly different among the three habitats (Figure 2). Seagrass substrates contained the lowest organic content and mangrove peat contained the highest. Seagrass sediments were primarily sand, while non-vegetated mud and mangrove substrates contained increased proportions of silt and clay. The high organic content of mangrove habitats likely reflects its fine particle nature as well as the dense mat of living and dead root materials.

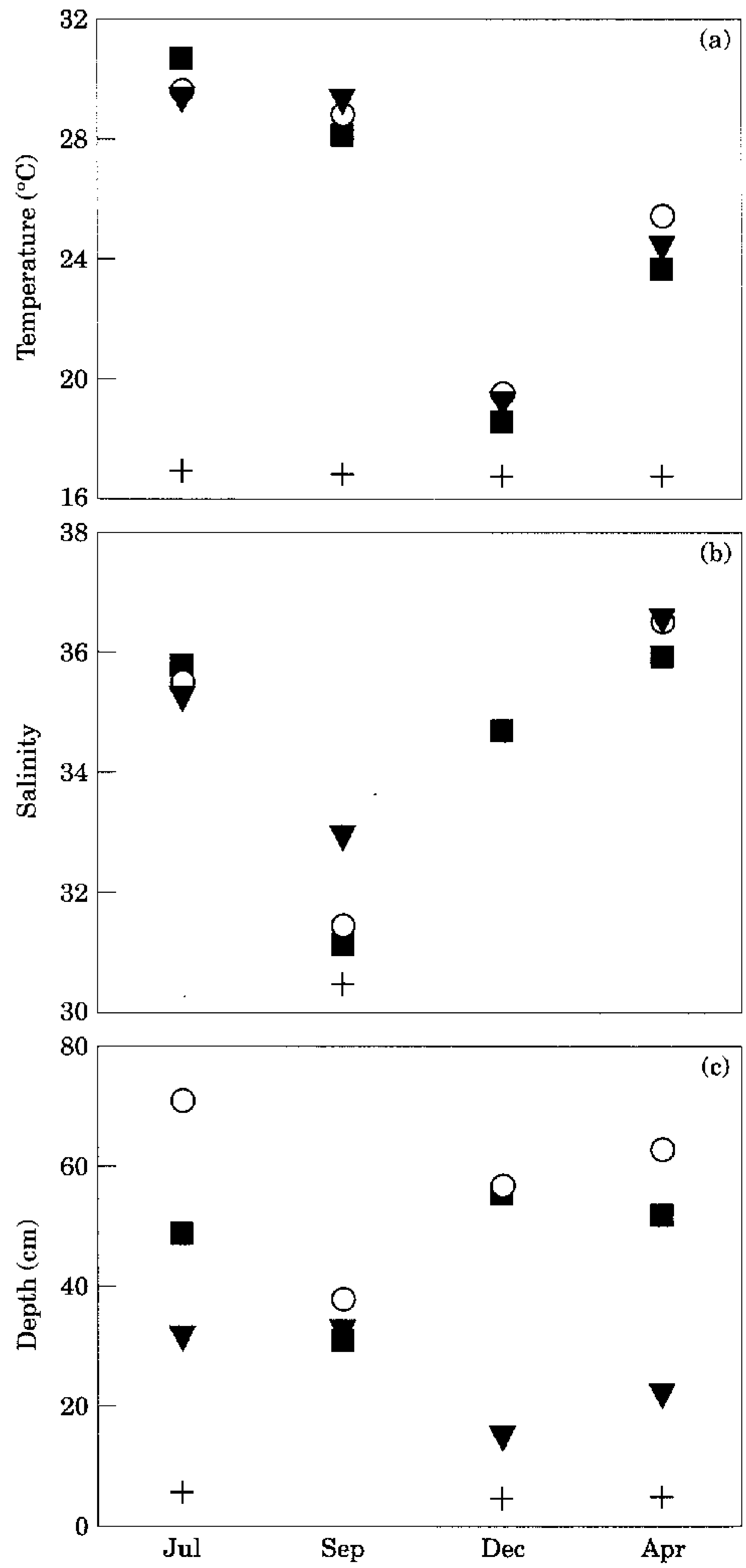

FIGURE 1. Rookery Bay, mean habitat characteristics: (a) water temperature, (b) salinity, (c) depth. +, significant differences among habitats ($P<0{\cdot}05$); ▼, mangrove; ○, non-vegetated; ■, seagrass.

Mangrove ecosystem benthos

Over 300 taxa of benthic organisms were recorded among 17 556 individuals from 102 cores (Appendix A). Some individuals were categorized only to family or genus (particularly polychaetes) and likely were larval, juvenile or damaged forms otherwise identifiable to species. Other organisms, including oligochaetes, nematodes, sipunculids, turbellarians and phoronids, were only identified to phylum, class or order and may have consisted of more than one species. Annelids account for 230 taxa alone, followed by amphipods with 30 taxa (Appendix A). However, 177 taxa each consisted of fewer than five individuals captured during the entire study. Dominant organisms (with total abundances in parentheses) were the tanaids *Hargeria rapax* (4706) and *Halmyrapseudes bahamensis* (732), oligochaetes (3858), and the polychaetes *Streblospio benedicti* (700), *Tharyx annulosus* (565) and *Mediomastus californiensis* (549). Seagrass provided the most heterogeneous habitat resulting in 193 taxa, followed by non-vegetated mud (155 taxa) and mangroves (87 taxa). Nearly 200 taxa, including many of the rare forms, were found in only one

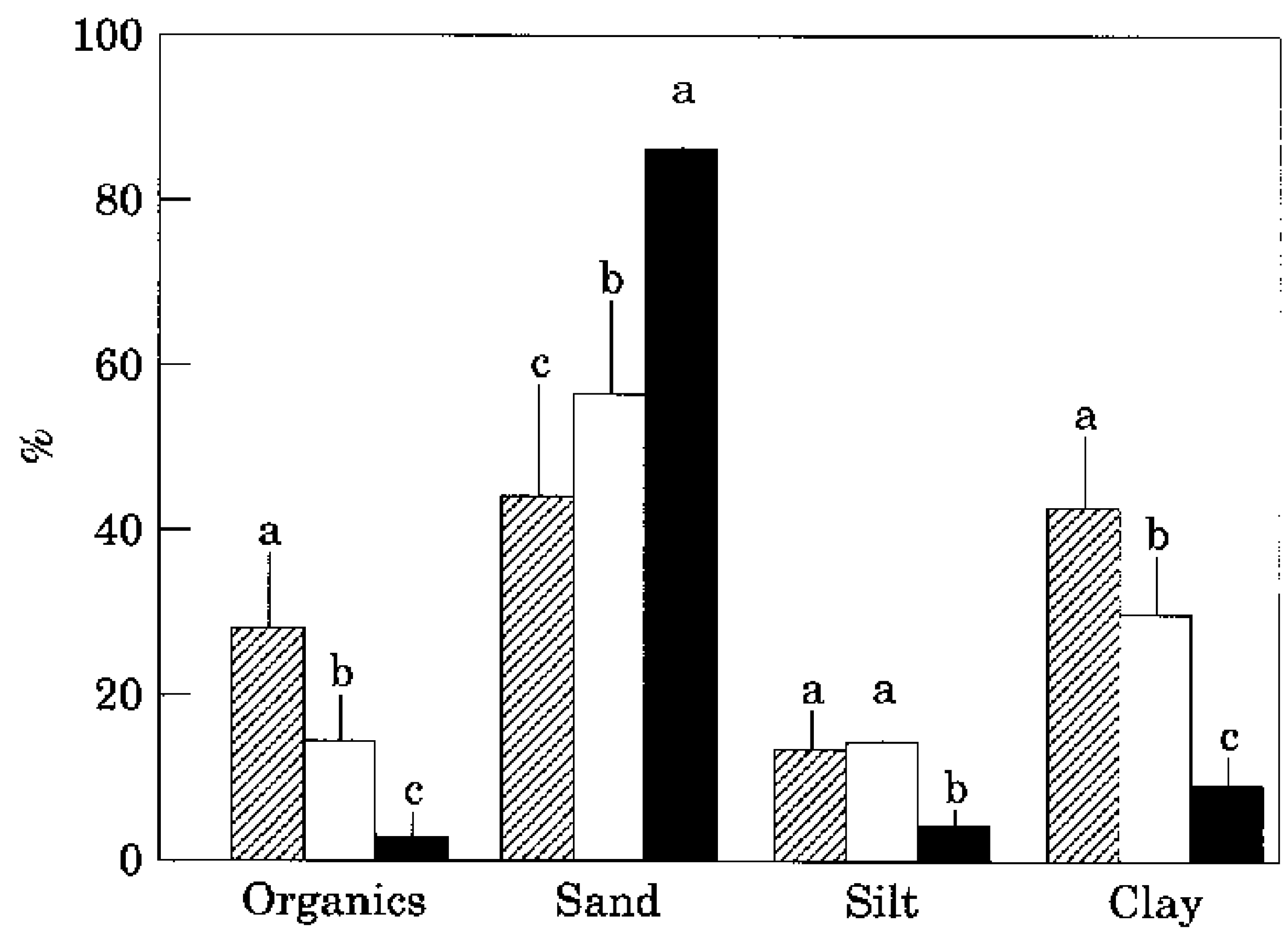

FIGURE 2. Rookery Bay, mean sediment organic content and sand, silt and clay proportions (%). $n=26$ cores habitat^{-1} pooled over three samplings (July, September, April). Vertical bar=standard deviation. Means indicated with differing letters were significantly different (Ryan's Q, $\alpha=0{\cdot}05$). Hatched bars, mangrove; open bars, non-vegetated; solid bars, seagrass.

habitat, while 31 taxa were found in all three habitats (Appendix A).

Major phyletic groups

Significant habitat or time effects on densities were detected for all major phyletic groups, total fauna and species richness (Table 1). Variation in densities of Annelida and Miscellaneous taxa was related to time: annelids were significantly more abundant in December and April than at other times, while the Miscellaneous group was significantly reduced in September (Figure 3). Maximum mean density of annelids in any habitat (31 388 m^{-2}) was recorded from mangroves in December. Variation in densities of Tanaidacea and Isopoda were related to the mangrove habitat, where tanaids were very dense and isopods were absent (Figure 3). Tanaid densities reached a maximum of 35 127 m^{-2} in mangroves during April. Amphipoda, Mollusca and total benthos densities all exhibited significant habitat × time interactions, as did species richness (Table 1). Amphipod and total benthos densities were highest in non-vegetated muds and seagrasses, but peaks occurred at different times in non-vegetated mud (September and December) than in seagrass (December and April; Figure 4). Maximum density of amphipods was 5123 m^{-2} in non-vegetated mud during December. Maximum densities of the total community were observed in mangroves during December (50 463 m^{-2}) and April (52 914 m^{-2}), coinciding with previously noted peaks in annelids and tanaids. In fact, total benthos densities in mangroves exceeded those in adjacent seagrasses and non-vegetated mud during all times examined (Figure 4). Peaks in mollusc densities and in species richness generally were observed in seagrasses and in December and April (Figure 4)). Maximum mollusc density was 1432 m^{-2} in seagrass during April.

Significant habitat or time effects on biomasses also were detected for total fauna and all major phyletic groups except isopods (Table 1). Tanaid biomass was significantly higher in mangroves than elsewhere, in conjunction with the previously mentioned high densities, whereas Miscellaneous biomasses were significantly lower in mangroves (Figure 5) due to the absence of the relatively large but rare ophiuroid *Ophiophragmus wurdemanni*. Amphipod and mollusc

TABLE 1. Results of two-way ANOVA comparisons of the effects of habitat and time on density and biomass of major benthic taxa in Rookery Bay, Florida

	Significance levels of two-way ANOVA					
	Density			Biomass		
	Habitat	Time	Interaction	Habitat	Time	Interaction
Annelida	NS	‡	NS	*	*	NS
Miscellaneous	NS	†	NS	*	NS	NS
Tanaidacea	‡	NS	NS	‡	NS	NS
Isopoda	†	NS	NS	NS	NS	NS
Amphipoda	‡	†	‡	‡	†	‡
Mollusca	‡	‡	†	‡	*	‡
Total benthos	‡	‡	NS	‡	*	NS
Species richness	‡	‡	‡	–	–	–

Three habitats (red mangrove, non-vegetated mud, seagrass) were sampled in July, September and December 1988, and April 1989. $n=8$ cores habitat^{-1} time period^{-1}, except $n=10$ in September. Significance levels indicated by: $*P\leq0{\cdot}05$, $\dagger P\leq0{\cdot}01$, $\ddagger P\leq0{\cdot}001$, NS $P>0{\cdot}05$.

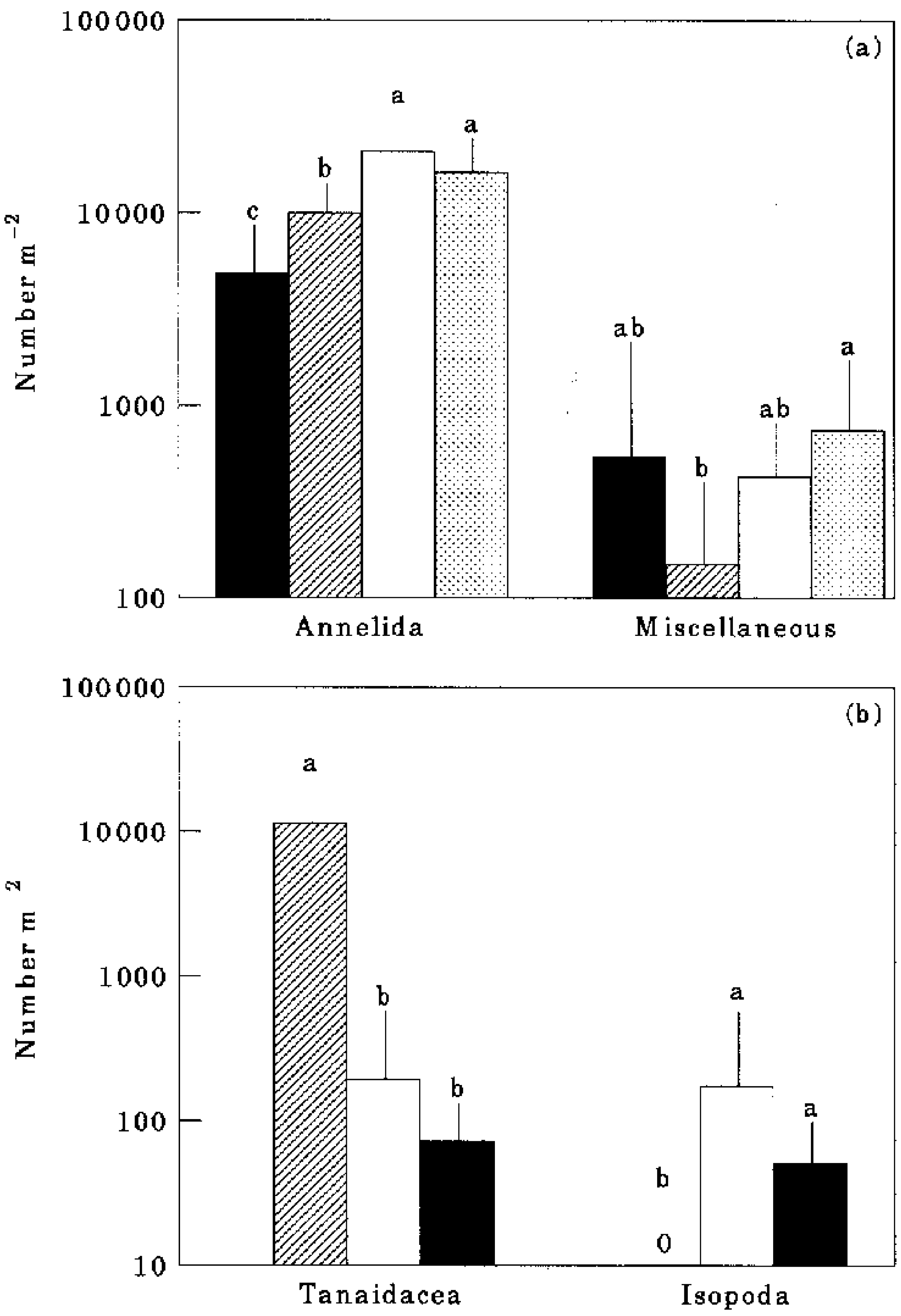

FIGURE 3. Rookery Bay, mean densities of benthic taxa: (a) time effect on Annelida and Miscellaneous, $n=24$ cores time period^{-1} except $n=30$ in September, and (b) habitat effect on Tanaidacea and Isopoda, $n=34$ cores habitat^{-1}. Vertical bar=standard deviation. Means indicated with differing letters were significantly different (Ryan's Q, $\alpha=0{\cdot}05$). (a) Solid bars, July; hatched bars, September; open bars, December; stippled bars, April. (b) hatched bars, mangrove; open bars, non-vegetated; solid bars, seagrass.

biomasses were typically highest in seagrasses but high biomasses were not restricted to any particular time (Figure 6). Biomasses for the total benthic community, and for annelids which made up the largest proportion of that biomass, were highest in seagrass and non-vegetated mud in April (Figure 6). In part, this was due to large polychaetes occasionally found in seagrasses and non-vegetated mud, but not in mangroves. Maximum biomass ($87{\cdot}4\ \mathrm{g\,m^{-2}}$) was recorded from seagrass in April.

Dominant organisms

Most of the habitat × time interaction effects on densities of major phyletic groups were resolved with increased taxonomic resolution. Of 32 dominant taxa (those averaging ≥ 636 individuals $\mathrm{m^{-2}}$ or five core^{-1} in any habitat at a given time), habitat effects only were detected for densities of 20 taxa and neither habitat nor time effects were found for nine others (Table 2). Each habitat harboured four to eight taxa that were significantly more abundant there than in alternate habitats. Densities of the tanaids *Hargeria rapax* and *Halmyrapseudes bahamensis* and the polychaetes *Capitella capitata, Potamilla reniformis* and *Syllis cornuta* were significantly higher in mangroves than elsewhere (Table 2). *Hargeria rapax* reached the maximum observed density of any species at $32\,159\ \mathrm{m^{-2}}$ in mangroves during April. An additional seven taxa, including the insect *Anurida maritima,* the bivalve, *Sphenia antillensis,* and the polychaetes *Capitella* sp., unidentified Capitellidae, *Polydora caulleryi, Polydora* sp. A and *Pseudopolydora* sp. A, were found almost exclusively in mangroves, even though densities were not significantly different among habitats (Table 2). Non-vegetated mud was characterized by significantly higher densities of the amphipod *Bemlos unicornis* and the polychaetes *Salmacina* sp., *Caulleriella bioculata* and *C. zetlandica,* and by non-significantly higher densities of the amphipod *Corophium* cf. *acherusicum* (Table 2). Seagrasses supported significantly higher densities of the amphipods *Ampelisca holmesi* and *A. vadorum,* the bivalves *Abra aequalis* and *Tellina versicolor,* the polychaetes *Leitoscoloplos robustus, Prionospio heterobranchia* and *Streblospio benedicti,* and nemerteans, and non-significantly higher densities of unidentified Syllidae (Table 2). Three polychaetes (*Exogone dispar, Fabriciola trilobata, Tharyx annulosus*) were each associated with differing pairs of two habitats (Table 2).

Densities of three of the 32 dominant taxa were affected by the interaction of habitat and time (Table 2). Oligochaetes were present at relatively high densities in all habitats at all times, but densities were higher in mangroves than elsewhere and higher during December and April (Figure 7). Oligochaetes were among the three most abundant taxa in any habitat in any month and reached a maximum density of $13\,554\ \mathrm{m^{-2}}$ in mangroves during December. The importance of this dominance, however, is tempered by the lack of taxonomic resolution. The polychaete *Aricidae philbinae* was most numerous in seagrasses, almost absent from mangroves, and reached highest densities in April (Figure 7). The polychaete *Mediomastus californiensis* was associated with non-vegetated mud and seagrass, with density peaks in all time periods (Figure 7).

Guild analysis

The functional significance of the species composition of each habitat was examined through feeding guild

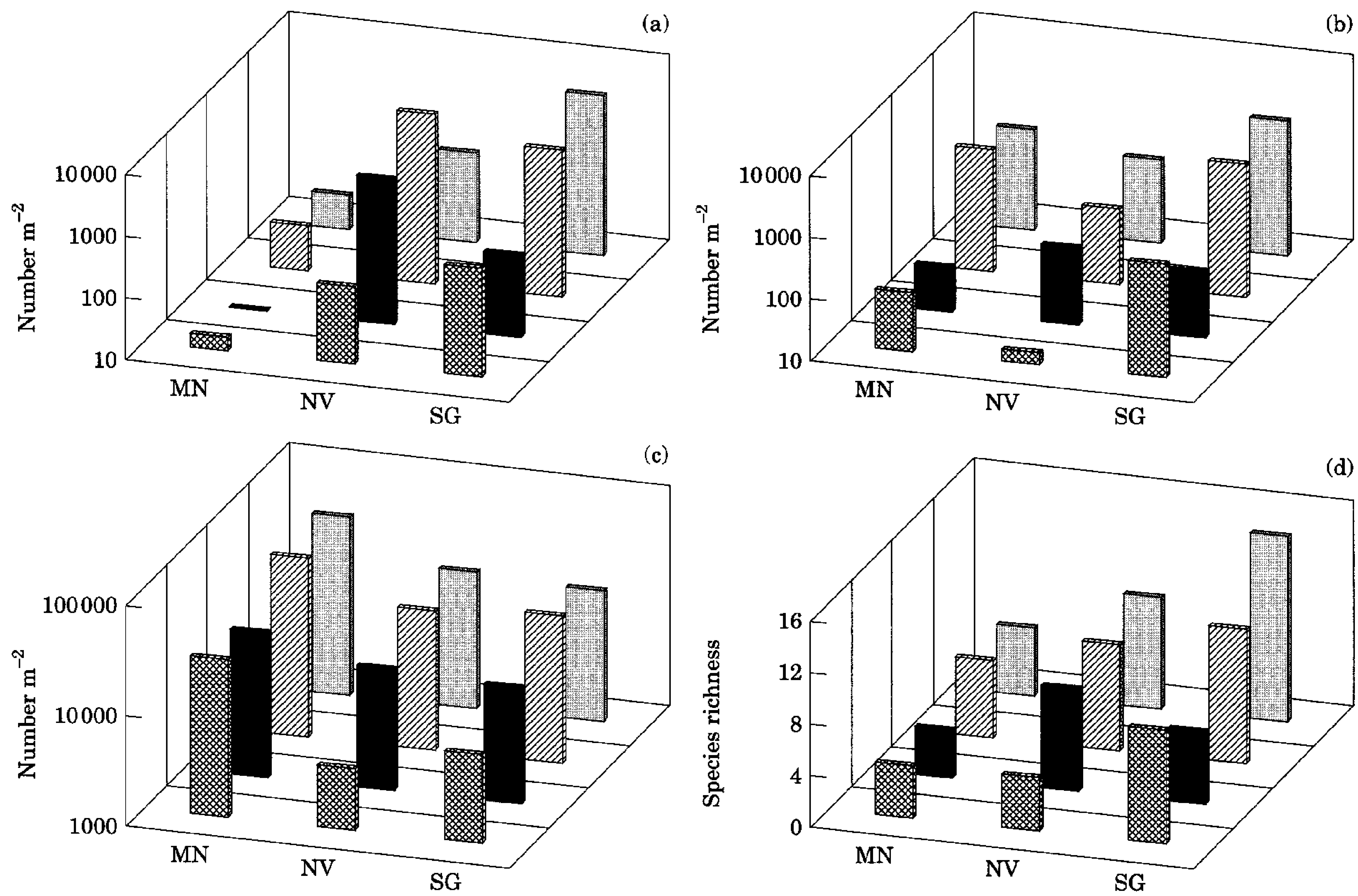

FIGURE 4. Rookery Bay, mean densities of benthic taxa illustrating habitat × time interaction: (a) Amphipoda, (b) Mollusca, (c) total benthos, and (d) species richness. MN, red mangrove; NV, non-vegetated mud; SG, seagrass, $n=8$ cores habitat^{-1} time period^{-1}, except $n=10$ in September. Stippled bars, April; hatched bars, December; solid bars, September; cross-hatched bars, July.

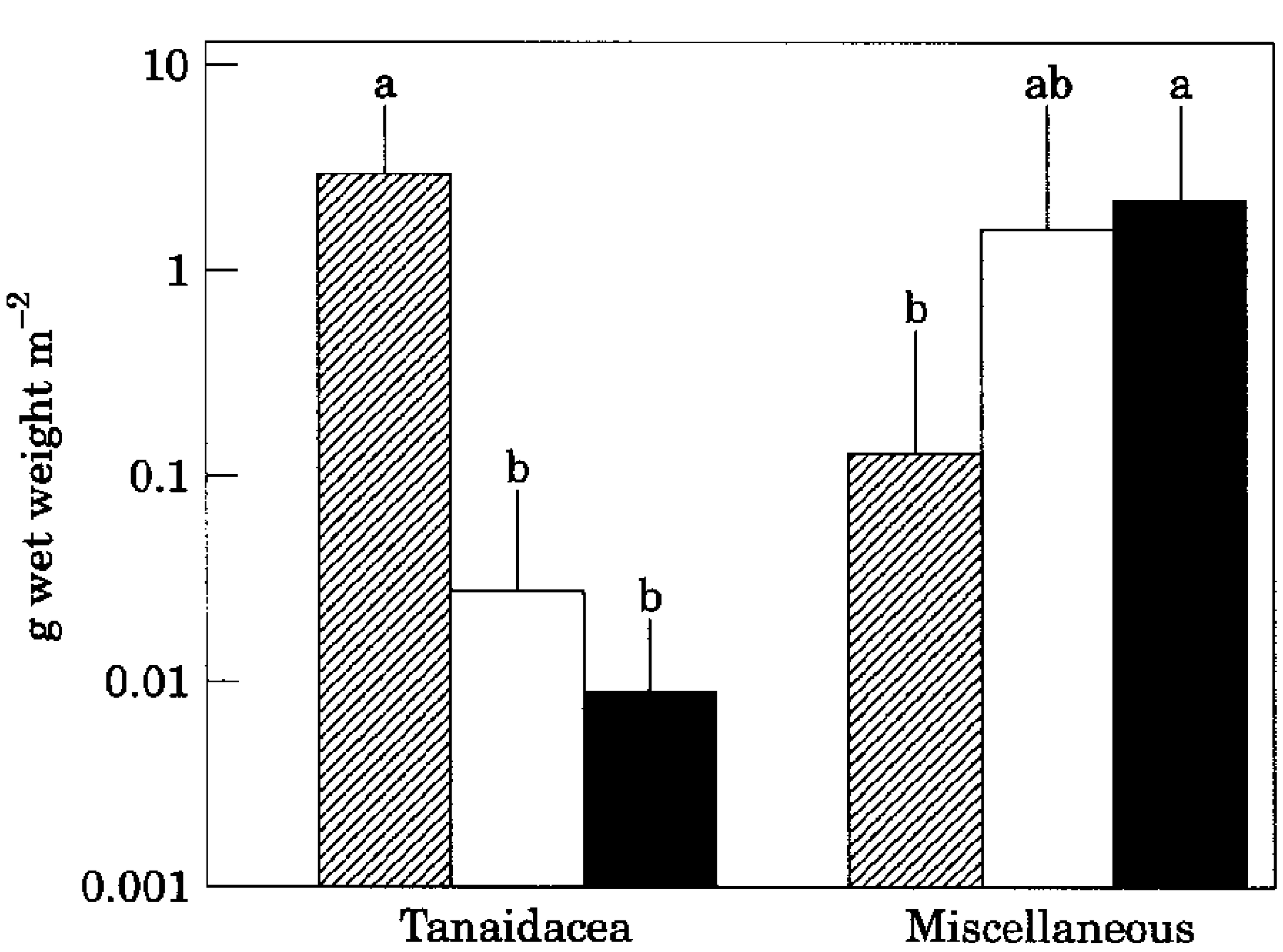

FIGURE 5. Rookery Bay, mean biomasses of Tanaidacea and Miscellaneous relative to habitat. $n=34$ cores habitat^{-1} pooled over four samplings. Vertical bar=standard deviation. Means indicated with differing letters were significantly different (Ryan's Q, $a=0{\cdot}05$). Hatched bars, mangrove; open bars, non-vegetated; solid bars, seagrass.

analysis of three assemblages: dominant taxa, taxa comprising 95% of the total number of individuals, and all taxa recorded in each habitat (Table 3). For all three assemblages, surface deposit feeders were the dominant guild, although they remained in consistently higher proportions in non-vegetated mud than in mangroves and seagrasses. Carnivores appeared to form similar proportions of the faunal assemblages in each habitat, except among the dominant taxa where no carnivores were found in non-vegetated mud. Rather, filter feeders were relatively abundant among dominant taxa in non- vegetated mud although they declined to third or fourth rank over all taxa in each habitat. Burrowers were more abundant in mangrove and seagrass habitats than in non-vegetated mud over all three sets of fauna, while herbivores were rare throughout the system (Table 3).

Discussion

Seagrasses, emergent marshes and their contiguous non-vegetated areas have received much attention

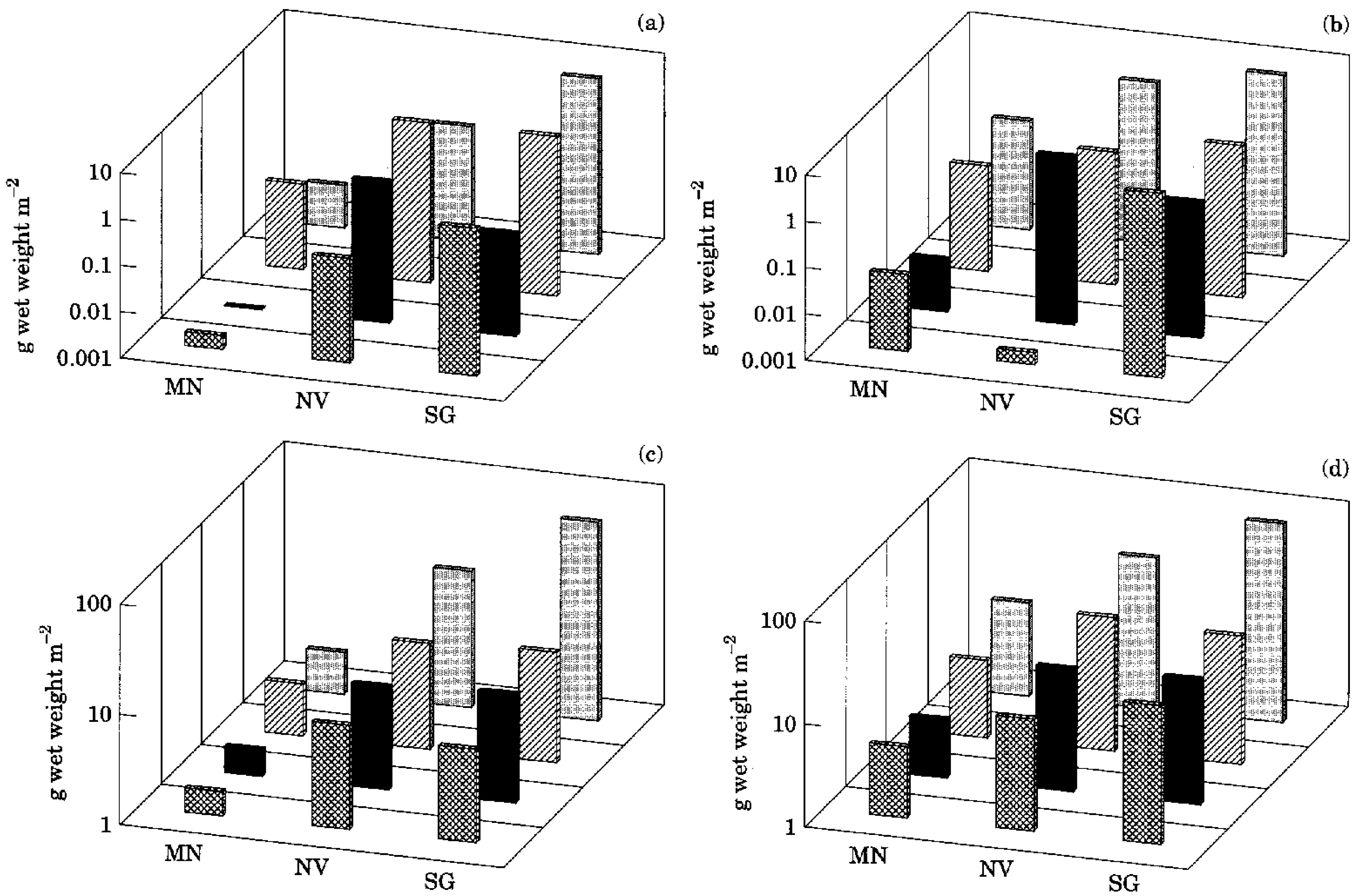

FIGURE 6. Rookery Bay, mean biomasses of benthic taxa illustrating habitat × time interactions: (a) Amphipoda, (b) Mollusca, (c) Annelida, and (d) total benthos. MN, red mangrove; NV, non-vegetated mud; SG, seagrass, n= 8 cores habitat^{-1} time period^{-1}, except n=10 in September. Stippled bars, April; hatched bars, December; solid bars, September; cross-hatched bars, July.

from estuarine researchers attempting to ascertain the values of these habitats to fishery and forage organisms. The role of mangroves in supporting secondary productivity remains poorly quantified (Alongi, 1989; Lee, 1995). The present study has shown that red mangroves exhibit at least one of the characteristics that make vegetated habitats valuable to fishery and forage organisms, namely high densities of potential prey. Total benthic population densities in mangroves exceeded those in adjacent seagrasses and non-vegetated mud during all times examined. Mangrove benthos densities, ranging from 22 591 m^{-2} in September to 52 914 m^{-2} in April, equal or exceed those found in highly productive seagrass habitats elsewhere in the south-eastern United States (1859–38 780 m^{-2}; 0·5 mm sieves only, as reviewed by Virnstein, 1987).

There has been little published research comparing benthic faunal relationships among mangrove ecosystem habitats in Florida (Odum *et al.*, 1982; Mahadevan *et al.*, 1984; Continental Shelf Associates, Inc., 1990) or elsewhere (Alongi, 1989). Weinstein *et al.* (1977) described benthic invertebrates in seagrasses, tidal creeks and artificial canals surrounding Marco Island, a housing development in mangrove habitat south of Rookery Bay, without quantifying among-habitat differences in species composition and abundance. In addition, certain taxa abundant in Rookery Bay (such as tanaids) were not reported from Marco Island. Most research on benthic communities of mangrove ecosystems examines a single habitat. For example, both Guelorget *et al.* (1990) and Stoner and Acevedo (1990) examined non-vegetated mud benthos of mangrove-lined lagoons in the Caribbean without sampling among the mangroves. Hodda and Nicholas (1985), Alongi (1987) and Sasekumar (1994) reported densities of meiofauna (primarily nematodes and copepods) but only within intertidal mangrove zones of Australia and Malaysia.

Kolehmainen and Hildner (1975) compared benthic biomasses in Puerto Rico mangrove zones with those in adjacent seagrass zones, finding biomass was

TABLE 2. Results of ANOVA comparisons of dominant benthic faunal densities (taxa averaging ≥five individuals core^{-1} in any habitat at a given time) in Rookery Bay, Florida. Two-way ANOVA assessed the effects of habitat and time for taxa occurring in two to four sampling periods. One-way ANOVA assessed habitat effects for taxa dominant at only one time or when data were pooled for taxa having no time or interaction effects as indicated by two- way ANOVA

		Mean density (number m^{-2})			ANOVA	
Times	Taxa	MN	NV	SG	*F*	*P*
JSDA	*Capitella capitata*	1471a	168b	86b	22·96	0·001
	Halmyrapseudes bahamensis	2714a	8b	19b	43·75	0·001
	Hargeria rapax	17 331a	228b	56b	54·15	0·001
SD	*Potamilla reniformis*	2171a	28b	7b	14·33	0·001
	Bemlos unicornis	0b	2291a	149b	5·37	0·008
	Salmacina sp.	0b	1209a	0b	7·81	0·001
	Prionospio heterobranchia	0c	375b	1350a	66·29	0·001
	Streblospio benedicti	14c	1428b	3295a	39·19	0·001
DA	*Exogone dispar*	756a	80b	366ab	4·21	0·021
	Tharyx annulosus	24b	3357a	589a	13·21	0·001
	Ampelisca holmesi	0b	24b	1201a	30·67	0·001
J	*Anurida maritima*	1050	0	0	1·00	0·385
	Polydora sp. A	636	0	0	3·29	0·057
D	*Syllis cornuta*	1114a	0b	0b	16·27	0·001
	Fabriciola trilobata	1989a	16b	1098ab	4·09	0·032
	Capitella sp.	764	95	16	1·76	0·197
	Capitellidae	923	0	0	1·77	0·195
	Polydora caulleryi	1384	80	0	1·34	0·283
	Pseudopolydora sp. A	1209	16	32	1·59	0·228
	Sphenia antillensis	636	16	95	1·92	0·170
	Corophium cf. acherusicum	0	668	64	2·02	0·157
	Abra aequalis	0b	0b	700a	7·85	0·003
	Leitoscoloplos robustus	0b	0b	2021a	7·49	0·004
A	*Caulleriella bioculata*	16b	1798a	48b	27·72	0·001
	Caulleriella zetlandica	48b	2307a	16b	7·79	0·003
	Ampelisca vadorum	0b	16b	843a	15·36	0·001
	Nemertea	95b	159b	987a	5·47	0·012
	Tellina versicolor	0b	95b	891a	14·12	0·001
	Syllidae	0	0	843	1·00	0·385

Taxa with significant main and interaction effects

		Significance levels in ANOVA		
		Habitat	Time	Interaction
JSDA	Oligochaeta	0·001	0·001	0·007
	Aricidea philbinae	0·001	0·001	0·005
SDA	*Mediomastus californiensis*	0·001	0·001	0·025

Three habitats (red mangrove=MN, non-vegetated mud=NV, seagrass=SG) were sampled in July, September and December 1988 and in April 1989 (J, S, D, A, respectively). n=8 cores habitat^{-1} time period^{-1}, except n=10 in September. Means indicated with differing letters were significantly different (Ryan's Q, α=0·05).

6–60 times higher in seagrasses (386 g m^{-2}) than within mangroves (6–61 g m^{-2}); however, they did not treat species compositions or numerical abundances. Their biomass values are similar in range and magnitude to results of this study (15·8–87·4 g m^{-2} in seagrass *vs.* 3·6–8·2 g -m^{-2} in mangroves). Dye (1983) and Wells (1983, 1986)) conducted benthic studies comparing intertidal mangroves and adjacent mud flats. Dye (1983) reported that meiofaunal densities (primarily nematodes) at the edge of or within South African *Rhizophora* and *Avicennia* forests were higher than in mud flats seaward of the mangroves. He reported oligochaete densities up to 290 000 m^{-2} and polychaete densities up to 90 000 m^{-2} in

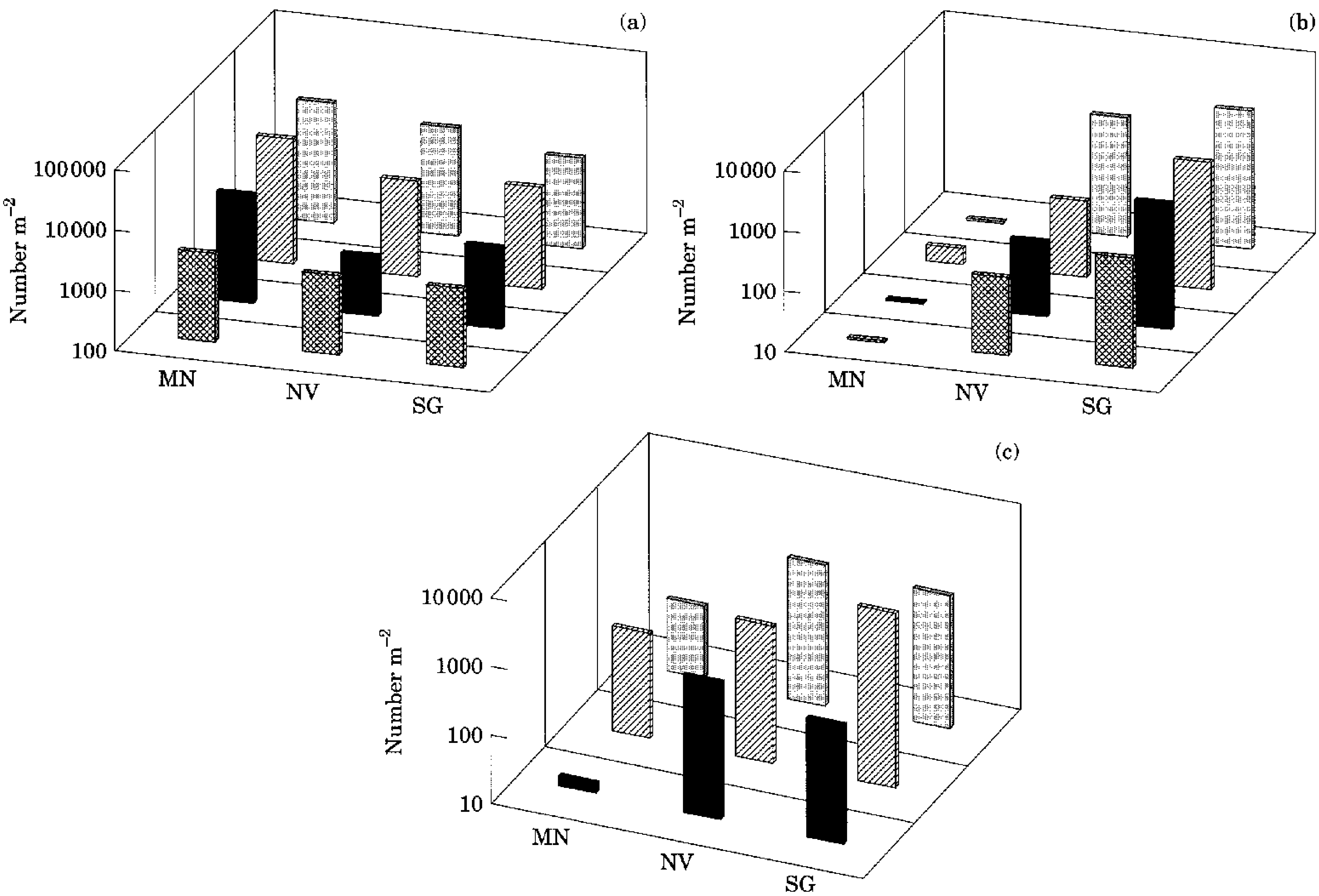

FIGURE 7. Rookery Bay, mean densities of benthic taxa illustrating habitat × time interactions: (a) Oligochaeta, (b) *Aricidea philbinae*, and (c) *Mediomastus californiensis*. MN, red mangrove; NV, non-vegetated mud; SG, seagrass. $n=8$ cores habitat^{-1} time period^{-1}, except $n=10$ in September. Stippled bars, April; hatched bars, December; solid bars, September; cross-hatched bars, July.

mangrove habitats. Wells (1983) first reported that mud flats supported higher infaunal and epifaunal densities (up to 992 m^{-2}) and more species than did adjacent *Rhizophora* and *Avicennia* mangrove substrates in Western Australia. But in a later study, Wells (1986) found that intertidal *Avicennia* substrates supported twice the density (up to 116 m^{-2}) and seven times the biomass (up to 21·6 g dry weight m^{-2}) of molluscs as did adjacent mud flats. These conflicting results probably stem from dissimilar sampling periods and sieve mesh sizes (September and 1 mm mesh in the first study, May–June and 2 mm mesh in the second). Unfortunately, none of these results are directly comparable since Kolehmainen and Hildner (1975) did not report sieve mesh size, Dye (1983) used 0·063 mm mesh, Wells (1983, 1986) used 1 mm or 2 mm mesh, and the present study used a 0·5 mm mesh. There is a need for studies using similar methods to compare structure of benthic communities in mangrove ecosystem habitats throughout the tropics.

Wells (1984) related benthic mollusc and crustacean abundances to feeding guilds. He found that filter feeders and deposit feeders dominated the mud flat, deposit feeders were most numerous in mangroves, and carnivores were relatively rare in either habitat. This suggested to Wells that the food web was based on the breakdown of mangrove detritus. Considering only molluscs and crustaceans, all three Rookery Bay habitats are dominated by surface deposit feeders while filter feeders are relatively rare; carnivores and burrowers only become important with the addition of annelids. The total benthic faunal community in Rookery Bay does not exhibit major differences in feeding guilds among habitats, even though there are differences in species composition. This community structure also suggests a mangrove detritus- driven system with high secondary productivity, as submitted by Odum and Heald (1972). A wide variety of fishes and invertebrates are associated with coastal mangroves (Gilmore & Snedaker, 1993; Lee, 1995; Thayer & Sheridan, 1997), but how they

TABLE 3. Distribution of taxa by feeding guild and habitat related to the number of taxa examined (dominant taxa from Table 2; other categories from Appendix A)

		Dominant taxa			95% of all taxa			All taxa		
	Guild	MP	NV	SG	MP	NV	SG	MP	NV	SG
Macrophages										
Herbivores	hdj	–	–	–	–	–	1	–	–	1
	hmj	–	–	–	–	–	1	1	3	1
Carnivores	cdj	–	–	–	–	–	1	–	–	6
	cmj	2	–	2	3	6	7	18	39	38
	cmx	–	–	1	–	2	2	4	5	7
Microphages										
Filter feeders	fdj	–	1	–	–	2	3	–	–	4
	fsp	–	–	–	–	–	2	–	2	2
	fst	1	1	–	1	2	4	12	12	13
Surface deposit feeders	sdj	–	1	2	–	2	5	–	5	7
	sdp	1	–	2	1	1	7	4	6	10
	sdt	4	2	4	4	10	12	12	25	24
	sdx	–	–	–	–	–	–	–	1	–
	smj	3	–	–	3	10	9	7	18	19
	smt	–	2	–	–	5	1	4	6	4
	smx	1	2	2	1	4	4	2	8	8
	sst	–	–	–	–	2	2	8	9	8
Burrowers	bmx	3	1	2	3	4	10	10	11	27
	bsx	–	–	–	1	–	5	1	2	11
All guilds		15	10	15	17	50	76	83	152	190

MP, mangrove peat; NV, non-vegetated mud; SG, seagrass. Feeding guilds indicated by three letter code: first letter (major food) -b=subsurface deposit feeder, c=carnivore, f=filter feeder, h=herbivore, s=surface deposit feeder; second letter (motility) -d=discretely motile, m=motile, s=sessile; third letter (feeding structure) -j=jaws, p=pump, t=tentacles, x=other, such as eversible pharynges (Fauchald & Jumars, 1979).

exploit the mangrove-based benthos remains unclear. For example, transfer of mangrove carbon to aquatic organisms seems limited to organisms occupying areas within or immediately adjacent to mangrove forests. Fleming *et al.* (1990) review data indicating that within 2 km of shore the isotopic signature of mangrove carbon in heterotrophs is lost to signatures characteristic of seagrass or algal carbon sources.

Intertidal vegetated habitats are thought to provide greater densities of food and greater degrees of refuge than non-vegetated habitats and to attract mobile organisms as these habitats become accessible. Comparative tests of the food hypothesis have been conducted for seagrasses *vs.* adjacent non-vegetated habitats. Densities of potential prey (infauna and epifauna) for fish and macro-invertebrate predators are usually higher in seagrass habitats than in non-vegetated mud (Virnstein *et al.*, 1983; Lewis, 1984; Sergeev *et al.*, 1988; Edgar, 1990; Ansari *et al.*, 1991), often due to higher predation outside of seagrasses (Robertson, 1984; Summerson & Peterson, 1984). In the present study, intertidal red mangrove habitats supported benthic faunal densities (particularly of tanaids and oligochaetes) comparable to or higher than those in adjacent seagrass and non-vegetated mud habitats. These high densities may be due to a variety of factors that may or may not be causally related to the presence of mangroves, including tidal height and duration of flooding, higher sediment organic content, smaller particle size and circulation patterns. The most obvious is protection afforded by limited duration flooding of mangroves relative to other substrates during high tides. At certain times of the year, however, fish and crab densities in flooded mangroves equal or exceed those in adjacent Rookery Bay habitats (Sheridan, 1992). Experiments testing whether mobile macrofauna are able to exploit these abundant food resources in mangroves have yet to be conducted, and low predation pressures could be responsible for high densities of benthic organisms found in red mangrove substrates. Tests of the refuge hypothesis conducted for seagrasses and non-vegetated mud indicate seagrass structure offers greater degrees of protection from predators (Wilcox *et al.*, 1975; Nelson, 1979; Heck & Thoman, 1981, 1984; Wilson *et al.*, 1987; Diehl, 1988). Tests of mangroves as refugia remain to be conducted. Comparative analyses of predation efficiency and use of prey types in relation to flooding duration among mangroves, non-vegetated mud and seagrasses are now needed to give a more complete understanding of the functions and values of intertidal mangrove habitats.

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Appendix A. Abundance of benthic fauna summed over 34 cores per habitat in Rookery Bay, Florida

		Habitats		
	Guild	MP	NV	SG
Amphipoda				
Ampelisca holmesi	sdj	–	3	156
Ampelisca vadorum	sdj	–	3	77
Ampithoe longimana	hdj	–	–	4
Aoridae	sdj	–	–	8
Batea catharinensis	smj	–	–	1
Batea cf. cuspidata	smj	–	–	3
Bemlos rectangulatus	sdj	–	7	–
Bemlos unicornis	sdj	–	332	44
Cerapus cf. benthophilus	fdj	–	–	4
Colomastix halichondriae	cmj	–	2	–
Colomastix sp.	cmj	–	1	–
Corophium cf. acherusicum	fdj	–	51	4
Corophium cf. simile	fdj	–	37	1
Cymadusa compta	hmj	–	1	63
Deutella cf. incerta	smj	1	–	7
Eobrolgus (?) sp. 1	smj	–	15	–
Eobrolgus (?) sp. 2	smj	–	3	1
Ericthonius brasiliensis	fdj	–	–	4
Eudevenopus honduranus	smj	–	–	1
Grandidierella bonnieroides	sdj	–	2	–
Hyale sp.	hmj	3	–	–
Lembos (Plesiolembos?) sp.	sdj	–	–	1
Listriella sp.	cmj	–	6	1
Lysianassa sp.	cmj	–	1	–
Lysianopsis cf. alba	cmj	1	–	6
Melita elongata	smj	–	47	9
Monoculodes nyei	smj	–	–	1
Photis sp.	sdj	–	–	2
Rudilemboides naglei	sdj	–	–	27
Unidentified	–	1	–	1
Isopoda				
Cirolana sp.	smj	–	30	–
Cyathura polita	smj	–	22	8
Dynamenella angulata	smj	–	2	–
Erichsonella attenuata	smj	–	–	5
Erichsonella filiformis	smj	–	–	3
Exosphaeroma diminuta	smj	–	1	–
Kupellonura sp.	smj	–	3	–
Paracerceis caudata	smj	–	1	–
Tanaidacea				
Halmyrapseudes bahamensis	smj	725	2	5
Hargeria rapax	smj	4630	61	15
Teleotanais gerlachi	smj	–	–	1
Mollusca				
Abra aequalis	sdp	–	3	56
Amygdalum papyrium	sdp	3	1	1
Anadara transversa	sdp	–	–	7
Cerithium atratum	smx	–	1	–
Chaetopleura apiculata	smx	–	5	–
Chione cancellata	sdp	–	1	5
Corbula swiftiana	sdp	–	2	–
Crepidula aculeata	fsp	–	6	–
Crepidula plana	fsp	–	2	7
Haminoea elegans	smx	–	–	5
Marginella apicina	smx	–	–	4
Mytilidae (larval)	–	10	1	–
Nuculana acuta	sdp	–	–	1
Parvilucina multilineata	sdp	1	–	18
Solemya velum	sdp	–	–	2
Sphenia antillensis	sdp	41	3	7
Tagelus divisus	sdp	12	–	3
Tellina versicolor	sdp	–	8	109
Unidentified larvae	–	6	2	5
Unidentified	–	10	3	5
Annelida				
Aglaophamus verrilli	cmj	–	–	4
Amaeana trilobata	sst	–	1	–
Ampharetidae	sst	–	–	1
Amphictene (?) sp.	bmx	–	–	1
Anaitides longipes	cmx	1	1	5
Anaitides mucosa	cmx	–	2	2
Ancystrosyllis jonesi	cmj	–	1	–
Ancystrosyllis sp. C	cmj	–	1	–
Aonides mayaguezensis	sdt	–	–	9
Apoprionospio pygmaea	sdt	–	–	3
Arabellidae	cmj	–	–	1
Arenicola sp.	sdx	–	1	–
Aricidea catherinae	smx	–	51	–
Aricidea fragilis	smx	–	–	2
Aricidea lopezi	smx	–	2	1
Aricidea philbinae	smx	1	92	330
Aricidea suecica	smx	–	14	3
Aricidae taylori	smx	–	–	2
Armandia agilis	bmx	–	–	2
Armandia maculata	bmx	–	–	5
Asychis elongatus	bsx	–	–	1
Asychis sp.	bsx	–	–	1
Axiothella cf. mucosa	bsx	–	–	4
Axiothella sp.	bsx	–	–	4
Axiothella sp. A	bsx	–	–	9
Boccardiella sp.	sdt	–	2	–
Branchosyllis exilis	cmj	–	4	–
Brania sp.	cmj	–	1	–
Capitella capitata	bmx	393	45	23
Capitella sp.	bmx	97	8	14
Capitellidae	bmx	61	1	1
Capitellidae Genus AH	bmx	–	–	1
Capitellides sp.	bmx	8	–	–
Capitomastus sp.	bmx	–	–	10
Caulleriella alata	smt	–	14	–
Caulleriella bioculatus	smt	1	150	10
Caulleriella sp.	smt	6	–	–
Caulleriella sp. B	smt	–	3	–
Caulleriella zetlandica	smt	3	160	2
Chaetozone sp. A	smt	1	41	1
Chone americana	fst	4	9	14
Chone sp.	fst	5	3	3
Chone sp. A	fst	3	–	2
Chone sp. B	fst	3	1	–
Chone sp. F	fst	11	2	–
Chone sp. H	fst	–	–	2
Chone sp. L	fst	–	1	–
Cirratulidae Genus B	smt	–	8	
Cirratulus sp.	smt	–	–	1
Cirrophorus forticirratus	smx	–	2	–
Clymenella torquata	bsx	–	–	1

Cossura heterochaeta	bmx	–	1	–
Cossura soyeri	bmx	–	–	3
Dispio uncinata	sdt	–	1	2
Drilonereis longa	cmj	1	1	1
Drilonereis sp.	cmj	–	1	–
Eteone lactea	cmx	–	–	1
Euchone sp.	fst	2	–	–
Euclymene sp.	bsx	–	–	1
Euclymene sp. B	bsx	–	–	7
Eunicidae	cmj	–	4	–
Eupolymnia nebulosa	sst	1	–	–
Exogone atlantica	cmj	17	–	–
Exogone dispar	cmj	112	13	47
Exogone sp. A	cmj	–	–	1
Exogone sp. B	cmj	13	4	–
Exogone sp. C	cmj	8	–	1
Exogone sp. D	cmj	19	–	–
Fabricia sp.	sdt	5	–	–
Fabriciola trilobata	sdt	190	10	91
Fimbriosthenelais hobbsi	cmj	–	–	1
Fimbriosthenelais sp. A	cmj	–	–	1
Glycera abranchiata	cdj	–	–	1
Glycera americana	cdj	–	–	2
Glycera sp.	cdj	–	–	1
Glycinde nordmanni	cdj	–	–	3
Glycinde solitaria	cdj	–	–	6
Gyptis brevipalpa	bmx	–	2	1
Haplosyllis spongicola	cmj	–	13	–
Harmothoe sp.	cmj	–	–	2
Hauchiella sp.	sst	–	5	–
Hesionides arenaria (?)	hmj	–	1	–
Heteromastides sp. A	bmx	1	–	–
Heteromastus sp.	bmx	16	1	–
Hydroides dianthus	fst	–	1	–
Isolda pulchella	sst	–		2
Janua sp.	fst	–	–	9
Jasminiera sp.	fst	2	–	–
Kinbergonuphis cf. cedroensis	cmj	–	–	1
Kinbergonuphis oligobranchiata	cmj	–	–	3
Kinbergonuphis orensanzi	cmj	–	–	2
Kinbergonuphis simoni	cmj	–	–	2
Laonice cirrata	sdt	–	7	1
Lanice conchilega	sst	1	–	–
Leitoscoloplos fragilis	bmx	–	–	13
Leitoscoloplos robustus	bmx	–	6	147
Leitoscoloplos sp.	bmx	–	–	1
Leodora laevis	fst	–	–	3
Lepidasthenia sp.	cmj	–	1	–
Lumbrineris inflata	cmj	–	–	1
Lumbrineris sp. B	cmj	–	12	7
Lumbrineris sp. E	cmj	–	3	–
Lumbrineris verrilli	cmj	–	1	8
Lysilla sp.	sst	–	35	–
Lysippe sp. B	sst	–	35	–
Macroclymene sp.	bsx	–	2	–
Magelona pettibonae	sdt	–	2	–
Maldane sp. A	bsx	–	–	1
Maldanidae	bsx	–	1	3
Malmgreniella sp. B	cmj	–	1	3
Marphysa sanguinea	cmj	–	1	–
Marphysa sp. E	cmj	–	4	–
Mediomastus californiensis	bmx	29	201	319
Megalomma sp.	fst	1	–	–
Melinna cristata	sst	–	–	1
Micromaldane sp.	bsx	54	–	5
Mooreonuphis pallidula	cmj	–	–	2
Myriochele oculata	bmx	–	1	3
Neanthes acuminata	smj	–	–	5
Neanthes micromma	smj	1	13	–
Neanthes succinea	smj	10	8	21
Nematonereis hebes	cmj	–	6	–
Neoamphitrite edwardsi	sst	1	–	–
Neoamphitrite sp. A	sst	2	–	–
Neoleprea sp. A	sst	1	–	–
Neoleprea sp. B	sst	–	1	–
Neomediomastus sp.	bmx	30	–	–
Nephtys cryptomma	cmj	–	–	1
Nephtys picta	cmj	–	–	1
Nereidae	cmj	5	41	9
Nereis falsa	cmj	–	–	2
Nereis riisi	cmj	–	1	–
Nicon (?) sp.	cmj	–	1	–
Nothria textor	cmj	–	–	3
Notomastus latericeus	bmx	–	–	1
Odontosyllis enopla	cmj	1	1	–
Oligochaeta	smx	2181	869	808
Ophelina acuminata	bmx	–	–	5
Ophelina cylindricaudata	bmx	–	–	2
Ophelina sp. E	bmx	–	–	1
Ophioglycera sp. A	cdj	–	–	2
Ophryotrocha sp.	cmj	5	36	–
Orbinia americana (?)	bmx	–	–	1
Orbinia riseri	bmx	8	–	1
Oriopsis (?) sp.	fst	–	1	–
Owenia aedificator	sdt	–	–	1
Owenia sp.	sdt	–	–	2
Parahesione sp.	bmx	–	1	–
Paramphinome sp.	cmx	–	4	3
Paraprionospio pinnata	sdt	–	4	6
Pectinaria regalis	bmx	–	–	1
Pettiboneae sp. A	cmj	–	–	1
Pholoe minuta	cmj	–	–	2
Phyllohartmania taylori (?)	cmj	–	1	–
Piromis roberti	sdt	–	1	2
Platynereis dumerilli	cmj	–	–	3
Podarke obscura	bmx	–	10	1
Polydora aggregata	sdt	–	1	–
Polydora caulleryi	sdt	90	5	–
Polydora cf. hoplura	sdt	–	2	–
Polydora socialis	sdt	1	27	2
Polydora sp. A	sdt	63	1	–
Polynoidae	cmj	–	–	1
Potamethus sp.	fst	–	–	1
Potamilla reniformis	fst	347	5	4
Potamilla sp.	fst	1	–	–
Potamilla sp. A	fst	–	–	1
Prionospio (Minuspio) sp. A	sdt	–	–	2
Prionospio cirrifera	sdt	–	46	15
Prionospio cristata	sdt	–	9	22
Prionospio heterobranchia	sdt	1	72	228
Prionospio lighti	sdt	–	–	1
Prionospio multibranchiata	sdt	–	25	–
Prionospio perkensi	sdt	–	–	8
Prionospio saldanha	sdt	–	–	1
Prionospio sp.	sdt	1	1	4
Prionospio steenstrupi	sdt	–	–	2
Proceraea sp.	cmj	–	–	1
Pseudopolydora sp. A	sdt	130	7	2
Ramphobranchium diversosetosum	cmj	–	–	1
Rullierineris sp.	cmj	–	1	–
Sabella melanostigma	fst	–	1	3
Sabella sp.	fst	1	–	–
Sabellaria floridensis	fst	–	4	–
Sabellidae	fst	–	1	2
Salmacina sp.	fst	–	173	–
Schistomeringos rudolphi	cmj	–	5	–
Scolelepis texana	sdt	–	1	–

Scoloplos acmeceps	bmx	–	–	6
Scoloplos rubra	bmx	–	–	2
Scoloplos sp. B	bmx	–	–	4
Scoloplos texana	bmx	7	–	–
Sigambra sp.	cmj	–	1	–
Sigambra tentaculata	cmj	–	1	–
Sphaerosyllis aciculata	cmj	–	–	2
Sphaerosyllis longicauda	cmj	47	–	2
Sphaerosyllis piriferopsis	cmj	2	1	–
Sphaerosyllis renaudae (?)	cmj	2	–	–
Sphaerosyllis taylori	cmj	–	–	1
Spionidae	sdt	–	1	–
Spiophanes bombyx	sdt	–	–	4
Spirorbidae	fst	1	–	–
Spirorbis laevis	fst	–	–	1
Sthenelais boa	cmj	–	–	1
Sthenelais sp.	cmj	–	–	2
Streblosoma hartmanae	sst	–	3	7
Streblosoma sp.	sst	–	–	1
Streblospio benedicti	sdt	5	213	482
Syllidae	cmj	–	2	53
Syllides fulvus	cmj	–	1	–
Syllis (Typosyllis) sp.	cmj	6	–	–
Syllis alternata	cmj	63	2	–
Syllis armillaris	cmj	1	–	–
Syllis cornuta	cmj	122	–	–
Syllis ferugina	cmj	–	2	–
Syllis gracilis	cmj	–	2	–
Syllis sp. A	cmj	21	2	–
Terebella rubra	sst	2	–	–
Terebellidae	sst	1	2	1
Terebellidae (Polycirrinae)	sst	–	1	–
Terebellidae Genus B	sst	–	1	–
Terebellides atlantis	sst	–	–	5
Terebellides distincta	sst	–	–	2
Tharyx annulosus	sdt	4	472	89
Tharyx marioni (?)	sdt	15	–	–
Tharyx sp.	sdt	1	1	–
Travisia hobsonae	bmx	–	–	1
Trichobranchidae	sst	3	–	–
Websterinereis sp.	cmj	–	–	2
Miscellaneous				
Almyracuma sp. (Cu)	smj	–	3	1
Anurida maritima (In)	smj	110	–	1
Ceratopogonidae (In)	smj	14	–	–
Glottidia pyramidata (Br)	fsp	–	–	1
Heteromysis sp. (My)	smj	–	15	–
Mysidopsis bahia (My)	smj	–	2	–
Ophiophragmus wurdemanni (Op)	smj	–	12	10
Oxyurostylus smithi (Cu)	smj	–	6	2
Nematoda	cmx	2	8	3
Nemertea	cmx	23	32	87
Sipunculida	sdt	–	4	13
Turbellaria	cmx	4	–	2
Phoronida	fst	–	–	8

MP, mangrove peat; NV, vegetated mud; SG, seagrass. Feeding guilds given in Table 3. Miscellaneous category includes Brachiopoda (Br), Cumacea (Cu), Insecta (In), Mysidacea (My) and Ophiuroidea (Op).